

Feeding Ecology of Blue Marlins, Dolphinfinh, Yellowfin Tuna, and Wahoos from the North Atlantic Ocean and Comparisons with Other Oceans

PAUL J. RUDERSHAUSEN,* JEFFREY A. BUCKEL, AND JASON EDWARDS

Center for Marine Sciences and Technology, Department of Biology, North Carolina State University,
303 College Circle, Morehead City, North Carolina 28557, USA

DAMON P. GANNON¹

Duke University Marine Laboratory, 135 Duke Marine Laboratory Road,
Beaufort, North Carolina 28516, USA

CHRISTOPHER M. BUTLER² AND TYLER W. AVERETT

Center for Marine Sciences and Technology, Department of Biology, North Carolina State University,
303 College Circle, Morehead City, North Carolina 28557, USA

Abstract.—We examined diet, dietary niche width, diet overlap, and prey size–predator size relationships of blue marlins *Makaira nigricans*, dolphinfinh *Coryphaena hippurus*, yellowfin tuna *Thunnus albacares*, and wahoos *Acanthocybium solandri* caught in the western North Atlantic Ocean during the Big Rock Blue Marlin Tournament (BRT) in 1998–2000 and 2003–2009 and dolphinfinh captured outside the BRT from 2002 to 2004. Scombrids were important prey of blue marlins, yellowfin tuna, and wahoos; other frequently consumed prey included cephalopods (for yellowfin tuna and wahoos) and exocoetids (for yellowfin tuna). Dolphinfinh diets included exocoetids, portunids, and conspecifics as important prey. Blue marlins and wahoos consumed relatively few prey species (i.e., low dietary niche width), while dolphinfinh had the highest dietary niche width; yellowfin tuna had intermediate niche width values. Maximum prey size increased with dolphinfinh size; however, the consumption of small prey associated with algae *Sargassum* spp. occurred across the full size range of dolphinfinh examined. Most interspecific diet overlap values with dolphinfinh were not significant; however, blue marlins, yellowfin tuna, and wahoos had significant diet overlap due to their reliance on scombrid prey. Prey types found in blue marlins, dolphinfinh, and wahoos were more consistent among BRT years than prey found in yellowfin tuna. The prey of yellowfin tuna and wahoos collected during BRT years correlated with historic (early 1980s) diet data from North Carolina, the Gulf of Mexico, and the Bahamas. Based on principal components analysis, diets from several oceans clustered together for blue marlins, dolphinfinh, yellowfin tuna, and wahoos. Although differences were found, the diets of each predator were largely consistent both temporally (e.g., over the past three decades in the Gulf Stream) and spatially (among oceans), despite potential effects of fishing or environmental changes.

Blue marlins *Makaira nigricans*, dolphinfinh *Coryphaena hippurus*, yellowfin tuna *Thunnus albacares*, and wahoos *Acanthocybium solandri* have relatively high energetic demands. Thus, these highly migratory species consume large amounts of tertiary production from pelagic food webs (Essington et al. 2002). In the Northwest Atlantic Ocean, these species support

valuable sport fisheries; in many years, dolphinfinh and yellowfin tuna represent about 50% of total recreational landings in North Carolina (NCDMF 2009). Dolphinfinh, yellowfin tuna, and wahoos also support commercial fisheries throughout their range. Exploitation of a fish species may permanently alter attributes of the population or ecosystem from which it is harvested (Botsford et al. 1997). For example, human removal of fish predators can have a cascading “top-down” effect on pelagic food webs (Cox et al. 2002; Essington et al. 2002). This illustrates the importance of understanding the trophic ecology of upper-level predators occupying North Atlantic waters off the East Coast of the United States. Regional fishery management councils have started taking an ecosystem-based approach to fisheries management (SAFMC 2003, 2009); describing the feeding ecology

* Corresponding author: pjruders@unity.ncsu.edu

¹ Present address: Bowdoin Scientific Station, Department of Biology, Bowdoin College, 6500 College Station, Brunswick, Maine 04011, USA.

² Present address: Gulf Coast Research Laboratory, Center for Fisheries Research and Development, University of Southern Mississippi, 703 East Beach Drive, Ocean Springs, Mississippi 39564, USA.

Received June 16, 2009; accepted April 1, 2010

Published online August 9, 2010

of fish predators is a critical component of this approach (Link 2002).

Due to their relatively low abundance and harvest restrictions, highly migratory species (especially the blue marlin) are difficult to sample. Aside from lists and counts of diet items from small samples of blue marlins (Krumholz and DeSylva 1958; Erdman 1962), the feeding ecology of this predator has not been rigorously examined in the North Atlantic Ocean or compared with dietary habits of other highly migratory fish predators. The feeding habits of dolphinfish, yellowfin tuna, and wahoos collected from this region were last studied in detail roughly three decades ago (Manooch and Hogarth 1983; Manooch and Mason 1983; Manooch et al. 1984). These studies each examined a single predator species and provided no quantitative comparisons of diet among species.

Here we present 10 years of feeding ecology data describing four sympatric fish predators: the blue marlin, wahoo, dolphinfish, and yellowfin tuna. These predators were collected annually from a specific region of the U.S. Atlantic coast during a 1-week fishing tournament. The tournament provides the opportunity to simultaneously sample the diets of four highly migratory fish species that have overlapping distributions and potentially overlapping diets in this region and time of year. Our specific objectives were to (1) describe the diet of each predator species by percent frequency and percent weight; (2) examine prey size–predator size relationships; (3) measure diet overlap between pairs of predator species; (4) compare diets from the current study with historic collections; and (5) compare our findings from the North Atlantic Ocean with results from diet studies conducted in other oceans.

Methods

Collection of samples.—The Big Rock Blue Marlin Tournament (BRT) is a 1-week sportfishing competition for blue marlins, dolphinfish, yellowfin tuna, and wahoos that begins in the second weekend of June each year in Morehead City, North Carolina. We sampled specimens of these four predator species landed by BRT participants from 1998 to 2000 and from 2003 to 2009. Blue marlins are released during most fishing tournaments and in the majority of cases during other fishing operations. Thus, this tournament is one of the few opportunities to sample all four predators simultaneously. Given the relative abundance and importance of dolphinfish to offshore commercial and recreational troll fisheries and the opportunity to sample dolphinfish as part of a separate project (for sampling details, see Schwenke and Buckel 2008), we

also analyzed diets of this species from samples collected year-round from May 2002 to May 2004 in the same general region from which the BRT samples were collected.

Fishing for the BRT occurred between 0900 and 1500 hours Eastern Daylight Time. Fishing for non-BRT dolphinfish also occurred during the day but without time restrictions. The area in which tournament participants were allowed to fish was between latitudes 33.50°N and 35.17°N; there were no restrictions on how far east or west the fishing occurred. The BRT fishing took place almost exclusively in the Gulf Stream (Captain D. Britt, Morehead City, personal communication). The area over which dolphinfish were collected outside of the BRT occurred roughly between latitudes 33.75°N and 34.5°N. All predators were captured by trolling with ballyhoos *Hemiramphus brasiliensis*, other dead bait, or artificial lures. The BRT was sampled for a total of 10 years (from 1998 to 2000 and from 2003 to 2009). Non-BRT dolphinfish stomachs were collected at portside cleaning stations in North Carolina during portions of three consecutive years: May–October 2002, March–November 2003, and January–May 2004.

The selectivity of the relatively large surface-trolled hooks targeting blue marlins during the BRT resulted in “bycatch” (e.g., dolphinfish, yellowfin tuna, and wahoos) that were larger than the average sizes commonly observed during directed trips in this area. The tournament rules rewarded fish size rather than numbers; this also led to samples biased towards larger fish. Non-BRT dolphinfish were not subject to this bias. Blue marlins sampled in this study had a relatively large minimum size due to federal (currently >251 cm lower jaw fork length [LJFL]) and tournament (currently >279 cm LJFL or 182 kg) minimum size requirements. Anglers are penalized if they bring blue marlins that do not meet tournament minimum size limits to the scales, but these fish were still sampled for stomach contents.

Predators were placed on ice (dolphinfish, yellowfin tuna, and wahoos) or were kept cool (blue marlins) immediately after capture. After a predator was measured dockside (total length [TL], cm), its stomach was excised and placed on ice. Within 24 h of collection, stomach contents were removed and identified while fresh or were preserved in 10% buffered formalin and identified at a later date.

Stomach content analyses and cumulative prey curves.—Prey items were measured (mm) for TL (fish and shrimp), mantle length (cephalopods), or carapace width (crabs) when the length could be directly measured or reasonably reconstructed. We used external morphology and published references (Wil-

liams 1984; Carpenter 2002) to identify fish and invertebrate prey.

From 2003 to 2009, individual prey items were blotted on a paper towel to remove excess moisture and weighed (wet weight [g]). The diet of each predator species was characterized by percent frequency of occurrence (%O; all 10 years) and percent wet weight (%W; 2003–2009). Percent frequency of occurrence was defined as the number of stomachs in which prey type i occurred (N_i) divided by the number of stomachs in which food was present (N ; i.e., %O $_i = [N_i/N] \times 100$; Hyslop 1980). Percent wet weight (%W = w_i/w , where w_i is the weight of prey type i and w is the total weight of all prey types) was calculated from all organic stomach contents. Bait used to catch predators was not included in these diet calculations. Both %O and %W calculations were used to conduct intra- and interspecific diet comparisons.

Relatively few blue marlins, yellowfin tuna, and wahoos were caught during the 10 years of this study. For this reason, cumulative prey curves were constructed to determine whether the sample size (across 10 years) was sufficient to describe the dietary trend of each predator species (Ferry and Cailliet 1996; Cortés 1997). While it is unrealistic to expect that sampling the 1-week BRT would capture the full dietary breadth of each predator in the Gulf Stream, we believe that prey curve analysis was useful to determine whether the numbers of predators collected from 10 BRTs adequately described the prey groups most frequently consumed during the BRT. For cumulative prey curve analysis, prey items were grouped into families for fishes and crustaceans and order for mollusks. This resulted in 11 prey groups for blue marlins and wahoos, 17 prey groups for yellowfin tuna, 34 prey groups for BRT dolphinfish, and 29 prey groups for non-BRT dolphinfish. We used a resampling procedure to randomize the contents of individual stomachs 1,000 times for each predator species (Bizzarro et al. 2006). The means and SDs of the cumulative number of unique prey types (y-axis) were then plotted against the number of nonempty predator stomachs (x-axis) pooled across all years to determine whether the curve had reached an asymptote. Linear regression analysis was used to fit a line to the last four data points of the cumulative prey curve. If the slope of that line was not significantly different from zero (t -test: $P > 0.05$), then it was concluded that an asymptote had been reached (Bizzarro et al. 2006).

Prey length–predator length relationships.—Prey length–predator length ratios (PPRs) were calculated for each predator species by using all measurable prey from each stomach. There was a sufficient sample of

measurable prey items to determine size-based feeding habits for dolphinfish predators by use of 5th, 50th, and 95th regression quantiles. The 5th and 95th quantiles were generated to estimate extremes of prey and predator length data and to test the significance of the slopes of each quantile (Scharf et al. 1998). Quantile regression analysis for dolphinfish was computed by combining individuals collected from BRT and non-BRT sampling.

Dietary niche width and diet overlap of four sympatric predators.—For this section and the next two Methods sections, all identifiable prey were aggregated into 12 categories for ease of analysis and interpretation; %O and %W were then recalculated for each of these categories. The 12 prey groups were chosen based on relative importance. Fish prey were grouped into families; only those families that were represented in at least 3 of the 10 BRT years were included. This resulted in nine families of fish prey: Balistidae (triggerfishes), Carangidae (jacks), Coryphaenidae (dolphinfishes), Diodontidae (porcupinefishes), Exocoetidae (flyingfishes), Monacanthidae (filefishes), Scombridae (mackerels), Syngnathidae (pipefishes), and Tetraodontidae (puffers). Minor fish prey families (those that occurred in ≤ 2 years) were grouped together into an “other fish” category for functional purposes; during the 1 or 2 years when these families did occur in predator diets, they were minor components of the overall diet (see Tables A.1–A.5). All of the invertebrates identified in stomachs of the four predator species were grouped into two classes: Cephalopoda and Crustacea. Unidentified fish or invertebrates, vegetation, and debris were not included in these 12 prey categories.

Dietary niche width was measured for each BRT-sampled predator species by using the Shannon–Wiener index (H'), which was calculated as

$$H' = \sum_{i=1}^S p_i \log(p_i),$$

where p_i is the proportion of the prey community that belongs to the i th prey taxon (S). For each predator species, H' was calculated using normalized %O and %W data.

Observed diet overlap or partitioning between pairs of predator species collected from the BRT used two data sets: normalized %O and %W. Observed diet overlap was computed via Schoener's index (α ; Schoener 1970), which is given by the equation

$$\alpha = 1.0 - 0.5 \times \sum |p_{ij} - p_{ik}|,$$

where j and k are the two predator species, p_{ij} is the proportional contribution of prey taxon i to the total

TABLE 1.—Published diet studies of blue marlins, dolphinfish, yellowfin tuna, and wahoos that were included in the worldwide principal component analysis (NR = data not reported from the study; BRT = Big Rock Blue Marlin Tournament; NA = North Atlantic; SA = South Atlantic; NP = North Pacific). Citation numbers refer to the numbers next to the symbols in Figure 4.

Predator	Author(s)	Year(s) of data collection	Ocean	Gear	Predator sample size	Mass (kg) or length (cm) range (total length [TL] or fork length [FL])	Citation number
Blue marlin	Abitia-Cardenas et al. 2000	1987–1989	NP	Rod and reel	204	88–334 kg	1
	Brock 1984	1981–1982	NP	Rod and reel	87	~50–330 kg	2
	Júnior et al. 2004	1992–1999	SA	Longline	24	100–330 cm FL	3
	Present study	2003–2009	NA	Rod and reel	72	282–421 cm TL	4
Dolphinfish	Manooch et al. 1984	1980–1981	NA	Rod and reel	2,632	25–153 cm FL	5
	Olson and Galván-Magaña 2002	1992–1994	NP	Purse seine	545	42–177 cm FL	6
	Rose and Hassler 1974	1961–1963	NA	Rod and reel	396	~45–128 cm FL	7
	Present study (BRT)	2003–2009	NA	Rod and reel	307	68–169 cm TL	8
Yellowfin tuna	Present study (non-BRT)	2002–2004	NA	Rod and reel	420	24–170 cm TL	9
	Dragovich and Potthoff 1972	1968	SA	Rod and reel	132	52–94 cm FL	10
	Manooch and Mason 1983	1980–1982	NA	Rod and reel	196	NR	11
	Olson and Boggs 1986	1970–1972	NP	Purse seine	NR	NR	12
Wahoo	Vaske et al. 2003	1994–2002	SA	Handline	395	46–148 cm FL	13
	Present study	2003–2009	NA	Rod and reel	63	83–163 cm TL	14
	Manooch and Hogarth 1983	1965–1981	NA	Rod and reel	885	NR	15
	Vaske et al. 2003	1994–2002	SA	Handline	411	63–167 cm FL	16
	Present study	2003–2009	NA	Rod and reel	101	100–187 cm TL	17

frequency or weight of prey items from predator species j , and p_{ik} is the proportional contribution of prey taxon i to the total frequency or weight of prey items from predator species k . This index varies from 0 (no overlap) to 1 (complete overlap). Schoener's index is appropriate in situations where data on prey availability are absent (Wallace 1981). For diet overlap calculations, we compared observed overlap with a null model created by generating 1,000 randomizations of the data and reshuffling zero data for each predator species before each iteration (Gotelli and Entsminger 2001). Null model simulations were run with Ecosim software (Gotelli and Entsminger 2001). We considered diet overlap values greater than 90% of the simulated index values to represent significant overlap between two predators.

Historic and Big Rock Blue Marlin Tournament diet comparisons.—Dolphinfish, yellowfin tuna, and wahoo diets were compared between BRT and historic data. Historic dolphinfish samples were collected in 1980 and 1981 from the western North Atlantic Ocean (waters east of a region from Florida to North Carolina) and Gulf of Mexico (Manooch et al. 1984). Historic yellowfin tuna samples were collected from 1980 to 1982 from the North Atlantic and Gulf of Mexico (Manooch and Mason 1983). Historic wahoo samples (reported as percent volume) were collected during 1980 and 1981 in the North Atlantic and Gulf of Mexico (Manooch and Hogarth 1983). The association between BRT and historic samples was tested with Spearman's rank correlation using %W data from each

period. We assumed a 1:1 ratio between percent volume and %W data for interdecadal comparisons (and for principal components analysis [PCA], described in the next section). Comparisons between present and historic diets were also made with non-BRT dolphinfish that we collected. As with predators we sampled, historic samples were collected during daylight by using trolled baits (C. S. Manooch III, Morehead City, personal communication). For the PCA of historic and present data sets and published studies worldwide (next section), we chose to use %W rather than %O data due to uncertainty in how %O was defined and presented in the published studies.

Principal components analyses of Big Rock Blue Marlin Tournament data and published studies.—We conducted PCA (De Crespín de Billy et al. 2000) on normalized %O and %W BRT data (hereafter, "%PCA") to determine interannual variation in diets of the four predators. Additionally, %PCA was used to examine temporal (historic and present) trends in the western North Atlantic Ocean and spatial trends among oceans using diet data (%W) from 17 data sets. For these published studies, predators were collected with a variety of gears and over multiple decades (Table 1).

We conducted %PCA by calculating a covariance matrix on proportional diet data that was column centered (De Crespín de Billy et al. 2000). Data obtained from each %PCA were used to make biplots (Ter Braak 1983); in these biplots, dominant prey were dispersed, while less-dominant prey were concentrated around the origin. The eigenvectors from principal

component axes 1 and 2 (PC1 and PC2) that represented prey locations on each biplot were used to weight proportional diet data to calculate x - and y -coordinates for each data set. In this way, similarities or differences in predator diets among years (BRT data) or among studies could be visualized (De Crespín de Billy et al. 2000). Predators located near the origin of the biplot either fed on all of the dominant prey types or on less-dominant prey types (De Crespín de Billy et al. 2000).

Results

Stomach Content Analyses and Cumulative Prey Curves

In total, 70 blue marlins (mean TL = 360 cm; range = 282–421 cm), 307 dolphinfish (mean TL = 139 cm; range = 68–169 cm), 62 yellowfin tuna (mean TL = 116 cm; range = 83–163 cm), and 101 wahoos (mean TL = 136 cm; range = 100–187 cm) were collected over the 10 years of BRT sampling. Across all years, 94% of blue marlin stomachs, 88% of BRT dolphinfish stomachs, 89% of yellowfin tuna stomachs, and 79% of wahoo stomachs contained prey. A total of 420 stomachs from non-BRT dolphinfish (mean TL = 85 cm; range = 24–170 cm) were collected from 2002 to 2004; 55% of these stomachs contained prey. For each BRT-sampled predator species and for non-BRT dolphinfish, the cumulative prey curve reached an asymptote (all $P > 0.05$; Figure 1A–E); while the number of predator stomachs was sufficient to describe blue marlin and dolphinfish diets, the marginally significant P -values for yellowfin tuna ($P = 0.051$) and wahoos ($P = 0.063$) indicate that new prey groups were still being consumed during the latest year of collections (2009).

As indicated by %O and %W, scombrid fishes, principally *Auxis* spp., were the most important prey of blue marlins and wahoos (Tables A.1, A.4) in BRT collections. Teuthids (squids) were of secondary importance for wahoos. Balistids, dolphinfish, diodontids, exocoetids, and portunids (crabs) were important prey of BRT dolphinfish based on %O, while exocoetids, balistids, dolphinfish, and portunids were important prey based on %W (Table A.2). *Sargassum* spp. algae were also found in high frequency in BRT dolphinfish. Important food items of BRT yellowfin tuna included exocoetids and teuthids based on %O and exocoetids and scombrids based on %W (Table A.3).

Non-BRT dolphinfish had diverse diets as measured by both %O and %W (Table A.5). Prey of these predators were chiefly associated with *Sargassum* and included monacanthids, diodontids, balistids, syngnathids, and portunids. Of all the non-BRT

dolphinfish prey taxa, exocoetids were one of the few prey types that were not regularly associated with *Sargassum*.

Prey Length–Predator Length Relationships

Sample sizes of dolphinfish predator and prey lengths were sufficient for regression quantiles to be computed for this predator species. The 50th quantile equation for dolphinfish was prey size (PREY) = $40.63 + [0.001 \times \text{predator size (PRED)}]$. The 5th quantile equation was $\text{PREY} = 5.22 + (0.011 \times \text{PRED})$, and the 95th quantile equation was $\text{PREY} = 20.60 + (0.143 \times \text{PRED})$. Although the median prey size did not change (50th quantile: $P = 0.792$) as a function of predator size, the minimum size (5th quantile: $P < 0.001$) and maximum size (95th quantile: $P = 0.003$) increased (Figure 2A). The numbers of measurable prey from yellowfin tuna, wahoos, and blue marlins were relatively small ($n \leq 49$); with the exception of three dolphinfish prey (~1,000 mm) eaten by blue marlins, the sizes of those prey overlapped with each other and with the prey of dolphinfish (Figure 2B). The mean PPR for each main prey type in dolphinfish stomachs was 0.074 for balistids ($n = 24$), 0.042 for diodontids ($n = 80$), 0.065 for monacanthids ($n = 165$), 0.022 for portunids ($n = 314$), 0.076 for tetraodontids ($n = 27$), and 0.094 for teuthids ($n = 26$; Figure 2A). The mean PPR for blue marlins, dolphinfish, yellowfin tuna, and wahoos (across all types of measurable prey) was 0.104 ($n = 37$), 0.053 ($n = 760$), 0.128 ($n = 49$), and 0.123 ($n = 8$), respectively (Figure 2B).

Dietary Niche Width and Diet Overlap of Four Sympatric Predators

Dietary niche width varied among predator species. Using normalized %O, H' was 0.980 for BRT dolphinfish, 0.740 for yellowfin tuna, 0.512 for wahoos, and 0.428 for blue marlins. Using %W, H' was 0.870 for dolphinfish, 0.515 for yellowfin tuna, 0.261 for blue marlins, and 0.084 for wahoos. Values of diet overlap varied between pairs of predator species and based on the metric used (Table 2). Using normalized %O, diet overlap between blue marlins and wahoos ($P < 0.001$) and between yellowfin tuna and wahoos ($P = 0.019$) was significantly greater than the null distribution. Using %W, diet overlap between blue marlins and wahoos ($P = 0.057$), blue marlins and yellowfin tuna ($P = 0.046$), and yellowfin tuna and wahoos ($P < 0.001$) was significantly greater than the null distribution. No other comparisons were significant ($P > 0.10$), suggesting that overlap values were not different from random.

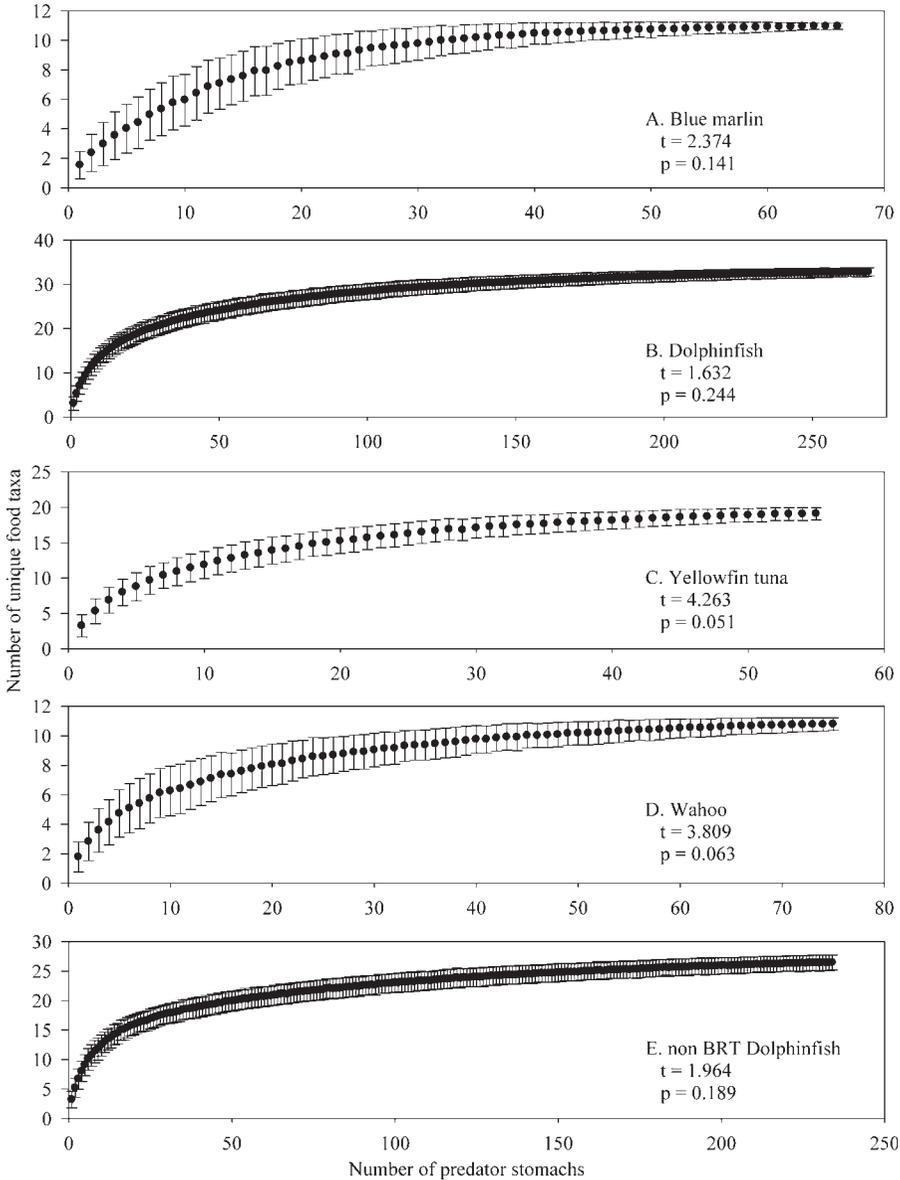


FIGURE 1.—Cumulative prey curves plotting mean (\pm SE) number of unique prey items (y-axis) against the number of stomachs (x-axis) sampled from predator species collected in the western North Atlantic: (A) blue marlins sampled during the Big Rock Blue Marlin Tournament (BRT), (B) BRT-sampled dolphinfish, (C) BRT-sampled yellowfin tuna, (D) BRT-sampled wahoos, and (E) dolphinfish sampled outside of the BRT (non-BRT dolphinfish). A nonsignificant t -statistic ($P > 0.05$) indicates that the prey curve reached an asymptote.

Historic and Big Rock Blue Marlin Tournament Diet Comparisons

Historic and BRT diets were not correlated for dolphinfish ($r = 0.182$, $P = 0.572$). The historic and BRT diets were correlated for yellowfin tuna ($r = 0.708$, $P = 0.010$) and wahoos ($r = 0.578$, $P = 0.049$). Diets of non-BRT dolphinfish were not correlated with

historic data ($r = 0.119$, $P = 0.713$). Results of %PCA of historic and present diet data are presented below.

Principal Components Analyses of Big Rock Blue Marlin Tournament Data and Published Studies

Biplots of the two BRT %PCAs displayed patterns that differed between metrics (normalized %O versus

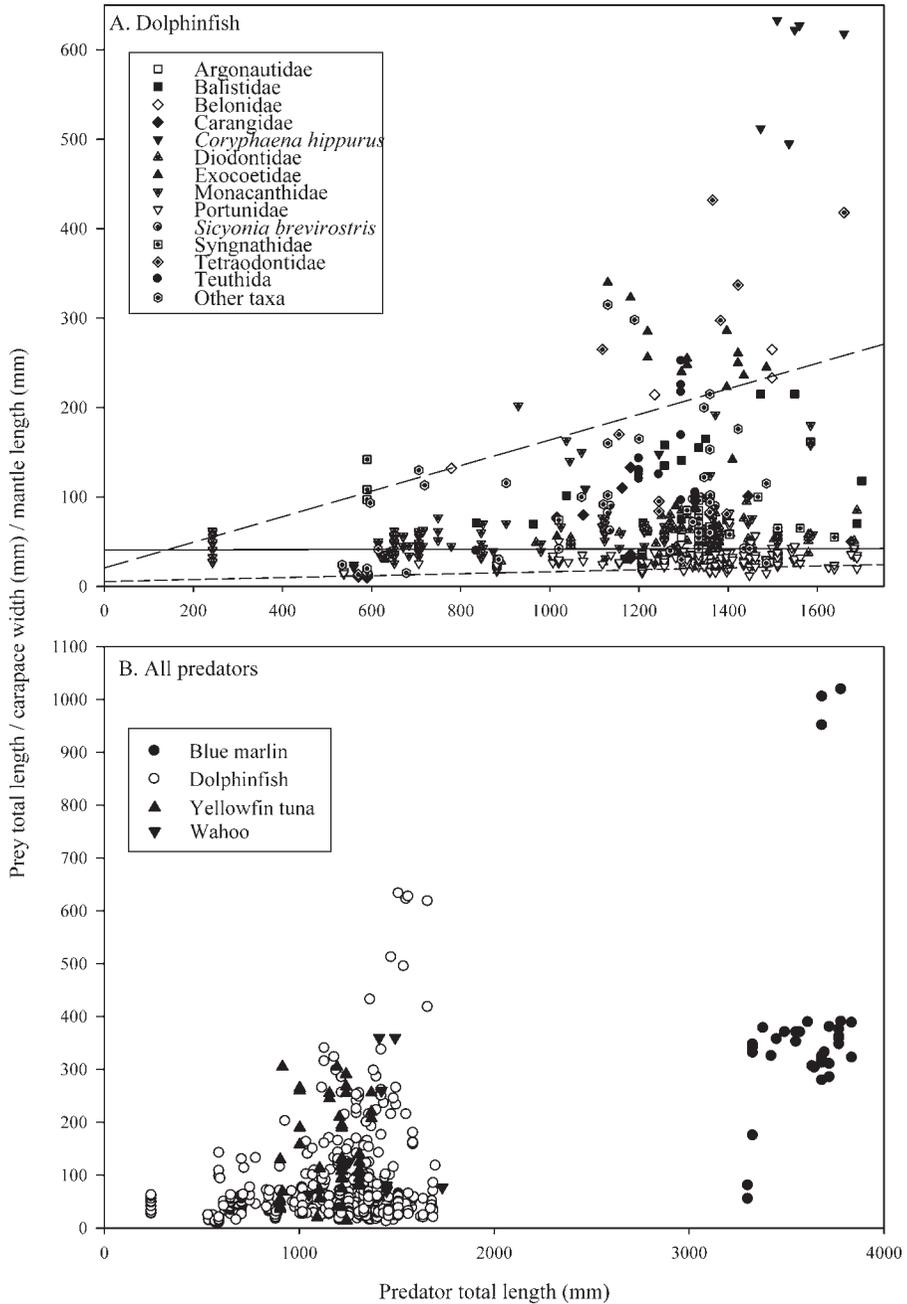


FIGURE 2.—Prey lengths (total length for fishes and shrimps, carapace width for crabs, and mantle length for cephalopods) in predator stomachs versus total length of (A) dolphinfish predators (number of prey measured = 760; *Coryphaena hippurus* = dolphinfish prey; *Sicyonia brevirostris* = rock shrimp; lower dashed line = 5th regression quantile, solid line = 50th quantile, upper dashed line = 95th quantile) and (B) all Big Rock Blue Marlin Tournament (BRT)-sampled predators combined (number of prey measured = 854; predators are the blue marlin, dolphinfish, yellowfin tuna, and wahoo). Different symbols represent prey in panel A and predators in panel B. The “other taxa” category in panel A includes the fish taxa Anguilliformes, southern stargazer *Astroscopeus y-graecum*, manefish *Caristius maderensis*, conger eel *Conger oceanicus*, flying gurnard *Dactylopterus volitans*, round herring *Etrumeus teres*, Bermuda chub *Kyphosus sectatrix*, Atlantic tripletail *Lobotes surinamensis*, Gulf butterfish *Peprilus burti*, Scombridae, and swordfish *Xiphias gladius* and three invertebrate taxa (Scyllaridae [slipper lobsters], octopus *Argonauta nodosa*, and sea skater *Halobates micans*).

TABLE 2.—Values of Schoener’s (1970) diet overlap index between predator species collected during the Big Rock Blue Marlin Tournament. Overlap was measured using two metrics: normalized percent frequency of occurrence (%O) and percent weight (%W). Values indicating overlap at an α of 0.10 are indicated by a single asterisk (*). Values indicating overlap at an α of 0.05 are indicated by two asterisks (**).

Metric and predator	Dolphinfish	Yellowfin tuna	Wahoo
%O			
Blue marlin	0.313	0.395	0.744**
Dolphinfish		0.502	0.320
Yellowfin tuna			0.591**
%W			
Blue marlin	0.326	0.475**	0.805*
Dolphinfish		0.361	0.179
Yellowfin tuna			0.471**

%W) and among predator species. For blue marlin and wahoo, years clustered more closely by %W than by %O. Cephalopods and scombrids were the dominant prey of BRT predators based on %O (dispersed away from the origin; Figure 3A), while cephalopods, exocoetids, and scombrids were the dominant prey based on %W (Figure 3B). Relatively less-important prey were clustered near the origin; these were mainly taxa associated with *Sargassum*. For %O BRT data, high scores on PC1 were associated with scombrids, while high scores on PC2 were associated with cephalopods. For %W BRT data, low scores on PC1 were associated with scombrids; high scores on PC2 were associated with exocoetids, and low scores were associated with cephalopods. Based on %O and %W, blue marlins and wahoos were grouped near scombrids, while dolphinfish were grouped near the origin. The PC1 and PC2 explained 55.6% and 21.1% of the variation in BRT %O data and 59.9% and 19.7% of the variation in BRT %W data.

The biplot from 17 worldwide data sets (Figure 4) showed a pattern fairly similar to the BRT %W biplot: cephalopods, exocoetids, and scombrids were dominant prey, with relatively less-important prey closer to the origin. High scores on PC1 were associated with scombrids, and low scores on PC1 were associated with exocoetids. On PC2, high scores were associated with exocoetids and scombrids, and low scores were associated with cephalopods. Blue marlins from the North Pacific and North Atlantic oceans were grouped near scombrids, while blue marlins from the South Atlantic Ocean were grouped between scombrids and cephalopods. Dolphinfish from all North Atlantic studies (including historic and present analyses) clustered relatively close to and generally above the origin, indicating reliance on rare prey and, to some extent, exocoetids and scombrids. Dolphinfish from the North Pacific Ocean were also located near the origin

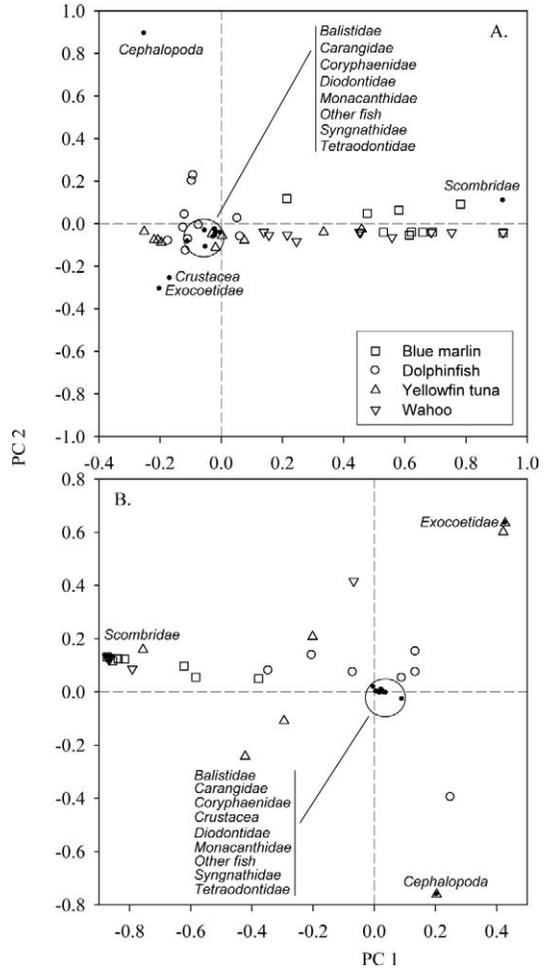


FIGURE 3.—Principal components analysis (%PCA) biplots of annual diet data from four predator species collected during the Big Rock Blue Marlin Tournament (BRT): (A) normalized percent frequency of occurrence (%O; recorded during 10 years: 1998–2000 and 2003–2009) and (B) percent weight (%W; recorded during 7 years: 2003–2009). Open symbols represent predator values. Black circles represent 12 prey taxa used to group diet data. The first and second principal component axes (PC1 and PC2) explained 55.6% and 21.1% of the variation in %O and 59.9% and 19.7% of the variation in %W.

due to reliance on rare and dominant prey, especially cephalopods. Yellowfin tuna data points were not tightly clustered due to high variability in dominant prey among studies within the North Atlantic Ocean (historic and present) and among oceans; dominant prey included exocoetids (South Atlantic), scombrids (North Pacific and North Atlantic), and cephalopods (South Atlantic). Wahoos from the two North Atlantic data sets (historic and present) were grouped fairly

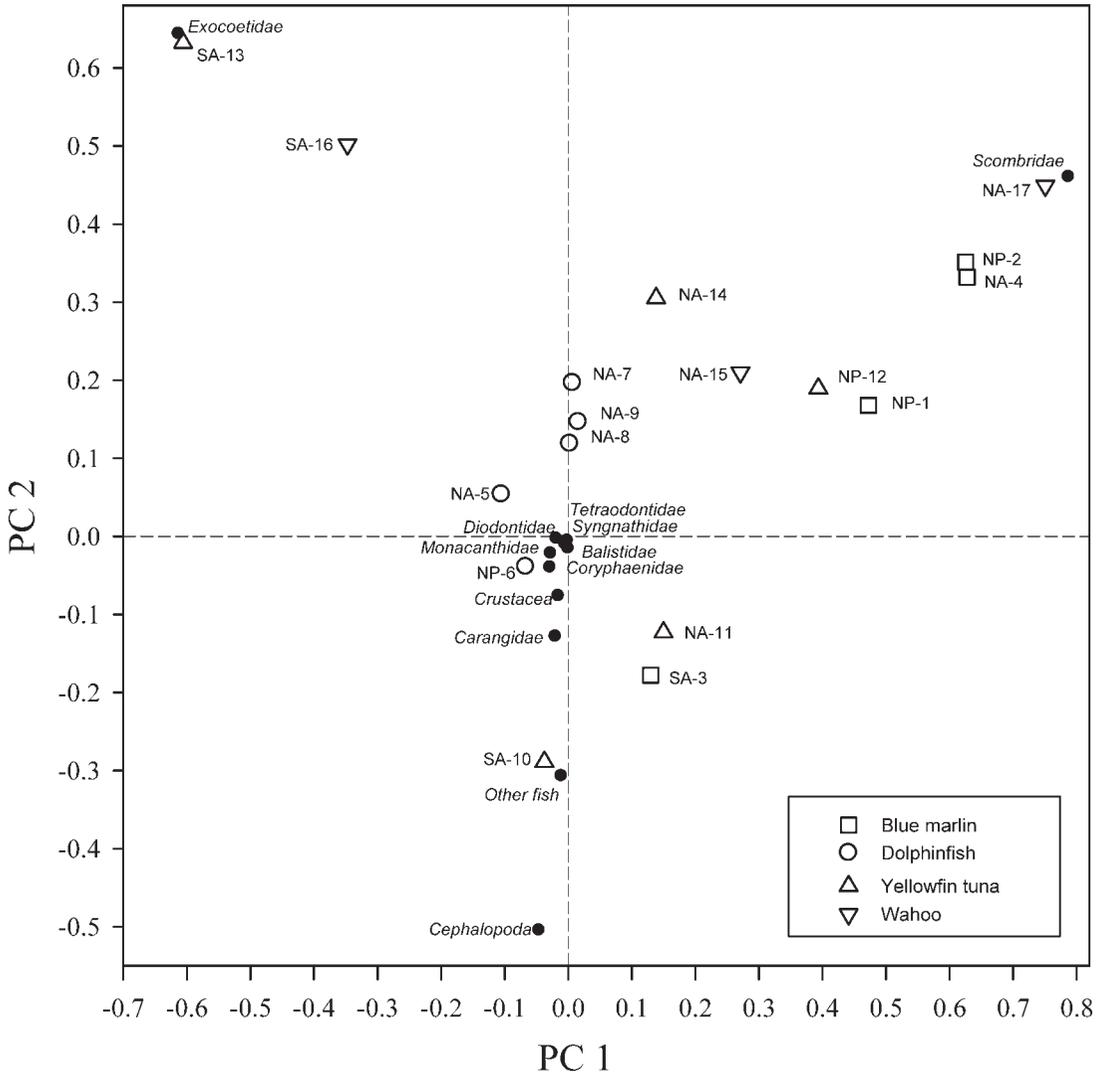


FIGURE 4.—Principal components analysis (%PCA) biplot of percent weight (%W) diet data from four predator species sampled during the Big Rock Blue Marlin Tournament (BRT), North Carolina; collected from North Carolina (2002–2004) outside the BRT (dolphinfish only); described in historical collections from the western North Atlantic; and described in other published data sets on dietary habits of these species in other oceans (17 data sets total; next to predator values [open symbols], codes correspond to citations in Table 1 and ocean of collection, where NA = North Atlantic, SA = South Atlantic, NP = North Pacific). See Methods for full description of historic and BRT data sets. Black circles represent 12 prey taxa used to group diet data. The first and second principal component axes (PC1 and PC2) explained 55.6% and 26.4% of the variation in the data.

closely to scombrids, while wahoos from the South Atlantic were grouped near exocoetids. The PC1 and PC2 explained 55.6% and 26.4%, respectively, of the variation in the worldwide data.

Discussion

Important Prey of Highly Migratory Species

Dominant prey of the four predators sampled during the BRT can be placed into three broad groups: (1)

prey associated with floating structure (e.g., *Sargassum* algae); (2) Exocoetidae, a family of tropical surface-schooling fishes that are not necessarily associated with floating structure (except during spawning: Evans 1961); and (3) schooling prey that may or may not be associated with surface waters—primarily *Auxis* spp. and cephalopods. Below, we discuss the importance of each prey group to the four predators studied.

Diets of blue marlins from the BRT were similar to

reports from other studies that identified scombrids as important prey for this predator (Erdman 1962; Baker 1966; Brock 1984; García de los Salmones et al. 1989; Abitia-Cardenas et al. 2000; Júnior et al. 2004). Several prey of the blue marlin, including teuthids, scombrids, and alepisaurids (lancetfishes), undertake diel vertical movements (Kishinouye 1923; Kubota and Uyeno 1970; Vecchione et al. 1989). Blue marlins are known to undertake vertical movements to the surface at night (Holland et al. 1990; Graves et al. 2002), and such diel movements may follow similar movements of their prey.

The dominant prey of BRT wahoos in Gulf Stream waters off North Carolina were scombrids and teuthids that can occur deeper in the water column. The only scombrid genus we identified from BRT wahoo stomachs was *Auxis* spp. There is little published information on the life history or ecology of this taxon (Carpenter 2002). Gaining a better understanding of the spatial distribution and population dynamics of *Auxis* spp. would aid in determining the spatial distribution and feeding ecology of blue marlins and wahoos.

The dominant prey of BRT yellowfin tuna were exocoetids, scombrids, and cephalopods. Yellowfin tuna are known to undergo ontogenetic shifts in habitat use and associated feeding strategies (Zavala-Camin 1981; Carey and Olson 1982; Maldeniya 1996; Grubbs and Holland 2003; Vaske et al. 2003; Graham et al. 2007). Graham et al. (2007) reported that yellowfin tuna exhibited a shift in diet at roughly 45 to 50 cm fork length (FL; ~52–58 cm TL). The average TL of yellowfin tuna from the BRT (116 cm) was larger than this ontogenetic shift size. Therefore, BRT yellowfin tuna diets are probably not representative of the diets of smaller yellowfin tuna in the North Atlantic Ocean.

Diets of BRT and non-BRT dolphinfish were highly diverse. This finding is consistent with other studies reporting that dolphinfish fed mostly on prey associated with floating structure (mainly *Sargassum* in the North Atlantic Ocean; Rose and Hassler 1974; Manooch and Nelson 1984; Massutí et al. 1998; Oxenford 1999; Olson and Galván-Magaña 2002). *Sargassum*-associated fishes and crustaceans include balistids, diodontids, syngnathids, monacanthids, and portunids (Fine 1970; Casazza and Ross 2008). The occurrence of *Sargassum* in the stomachs of many dolphinfish highlights the importance of structure-associated prey in their diet; it is likely that *Sargassum* spp. algae were incidentally consumed by predators while attacking prey (Manooch et al. 1984). Among the prey commonly found in BRT and non-BRT dolphinfish, exocoetids were the only ones that are not necessarily associated with *Sargassum*.

Cannibalism in dolphinfish has been observed in

several studies (Rose and Hassler 1974; Manooch et al. 1984; Olson and Galván-Magaña 2002). Cannibalism rates from dolphinfish collected outside the BRT (1.3% based on %O) were similar to rates in this region during the 1960s (3.8% based on %O; Rose and Hassler 1974) and during 1980 and 1981 (1.6% based on %O; Manooch et al. 1984). These historic studies did not report average lengths of the dolphinfish predators. However, the difference in the rates of cannibalism between the latter three data sets and the BRT dolphinfish data (10.1% based on %O) might be explained by predator size; dolphinfish from BRT collections (mean TL = 137 cm) were larger than those collected outside the BRT (mean TL = 85 cm). Cannibalized dolphinfish that could be measured from conspecific stomachs in BRT samples averaged 58 cm ($n = 7$), while their conspecific predators averaged 155 cm. The average PPR of dolphinfish feeding on conspecifics (0.278) is larger than the PPRs for other prey consumed by dolphinfish but similar to PPRs calculated for several species of cannibalizing gadoids (Juanes 2003).

We observed a wedge-shaped distribution of prey and predator sizes; this was also reported for dolphinfish captured from the eastern Pacific Ocean (EPO; Olson and Galván-Magaña 2002). Large predators often incorporate large prey into their diets while maintaining consumption of small prey (Juanes 1994; Scharf et al. 2000). Both the minimum prey size and the maximum prey size increased as dolphinfish size increased; this is potentially a consequence of increasingly large predators having larger gapes or foraging in open waters away from the small prey associated with *Sargassum* habitat (Rose and Hassler 1974). The average PPR for dolphinfish predators from the EPO was reported to be 0.177 (Olson and Galván-Magaña 2002) compared with the average PPR of 0.105 for dolphinfish in our study. The average predator size was similar in the two studies (88 cm FL [~107 cm TL] in the EPO study and 107 cm TL in our study). Thus, the difference in average PPR between these two studies might have arisen from the EPO dolphinfish predators consuming a greater proportion of prey not associated with structure; in the EPO, there is no algal habitat analogous to that created by *Sargassum* (R. J. Olson, La Jolla, California, personal communication).

To our knowledge, this is the first study to have compared diet overlap among these four predator species caught in the same time and area. Diet overlap was highest for pairs of BRT predators that consumed scombrids: the blue marlin and yellowfin tuna, blue marlin and wahoo, and yellowfin tuna and wahoo. The blue marlin, yellowfin tuna, and wahoo had narrower prey niche widths compared with the dolphinfish,

which had a broad niche width. The overlap value (Pianka's index = 0.59 for %*O* data) between dolphinfish and yellowfin tuna in the tropical Pacific Ocean (Moteki et al. 2001) is similar to our Schoener's index value of 0.50 for %*O*. Our Schoener's index value of 0.47 for %*W* is only about half of that observed for yellowfin tuna and wahoo overlap in the South Atlantic (Pianka's index = 0.90 for %*W* data; Vaske et al. 2003). Like Schoener's, Pianka's index ranges from 0 (no overlap) to 1 (complete overlap).

Temporal and Spatial Trends in Diets

There was interannual variability in BRT diets for all four species when %*O* was considered and for dolphinfish and yellowfin tuna when %*W* was considered. Thus, pooling data across years was necessary to gain a more complete understanding of diets during the BRT. However, blue marlins and wahoos had low interannual variability in diets due to consistent consumption of scombrids. Overall, despite low annual sample sizes, there was less interannual variability within each predator species than among species. Although we reviewed studies that collected predators over multiple years (Table 1), the authors of those studies did not quantify interannual variability in diets.

Pooled BRT sample sizes gave us the opportunity to compare diets of three species (dolphinfish, yellowfin tuna, and wahoo) with diets reported from historic studies in the North Atlantic Ocean. The BRT dolphinfish diets were not rank-correlated with historic collections, but these two data sets clustered on the %PCA biplot. The opposite pattern was observed for yellowfin tuna and wahoos, wherein historic and BRT diets were rank-correlated but were not closely clustered on the %PCA biplot. Generally, diets have remained consistent between decades in the North Atlantic Ocean; the most dominant prey (by %*W*) of dolphinfish (coryphaenids and exocoetids), wahoos (scombrids), and yellowfin tuna (exocoetids, scombrids, and cephalopods) were consistent between the two periods (Manooch and Hogarth 1983; Manooch and Mason 1983; Manooch et al. 1984).

Diet studies in different oceans generally clustered by predator species except for the wahoo and yellowfin tuna. The reliance of blue marlins on scombrids, especially *Auxis* spp., is consistent with investigations near New Zealand (Baker 1966), Hawaii (Brock 1984), the Caribbean (Krumholz and DeSylva 1958; Erdman 1962), and the greater Pacific Ocean (Abitia-Cardenas et al. 1999; Shimose et al. 2006). Dolphinfish from two oceans clustered closely on the biplot due to the highly diverse diets and overall similarity in prey proportion values (Rose and Hassler 1974; Manooch et al. 1984;

Olson and Galván-Magaña 2002; current study [BRT and non-BRT]). While wahoos have been found to feed on surface prey such as exocoetids (Manooch and Hogarth 1983; the present study), this prey type was more important to wahoos (and yellowfin tuna) from the South Atlantic Ocean (Vaske et al. 2003) than to wahoos in the North Atlantic. Diets of yellowfin tuna were closely related between BRT and North Pacific specimens (Olson and Boggs 1986) due to scombrid prey and were closely related between historic (Manooch and Mason 1983) and South Atlantic studies (Dragovich and Potthoff 1972) due to cephalopods.

Caveats and Implications

Feeding habits of predators collected during the BRT need to be evaluated in context of the time of year, time of day, and geographic region in which the tournament was held. The restrictive seasonal, diel, and geographic scales of sampling may not be representative of the diets of these species in other seasons or other regions. Additionally, care should be taken when considering fishing tournaments as a sole source of diet information, given the bias towards large fish. While diets of the four predators in this study need to be described in the context of the BRT's timing and location, our findings are novel in that they have allowed us to examine the diets of these four important ocean predators simultaneously. Long-term monitoring of predator diets might allow for detection of ecosystem change in this region of the Gulf Stream.

Removals of predators can have consequences that cascade down multiple trophic levels (Baum and Worm 2009). Additionally, declines in predator abundance have resulted in fishing at lower trophic levels (Pauly et al. 2002; Myers and Worm 2003; but see Essington et al. 2002). Despite these reports of ecosystem-level changes, we found little evidence for substantial temporal changes in the diets of dolphinfish, yellowfin tuna, or wahoos in the North Atlantic Ocean. Our finding of largely consistent predator diets over roughly three decades may indicate temporal stability in the relative abundance of their prey; it is unknown whether this finding is due to temporal stability in the abundance of these four predators. Interestingly, Sibert et al. (2006) found that the trophic level of exploited Pacific tuna populations was consistent over roughly six decades. Our results suggest a stable pelagic food web and forage base in waters of the Gulf Stream and reliance on prey types similar to those in other areas of the world.

Acknowledgments

This work was funded by the BRT and North Carolina Sea Grant (A/EA-22B). We thank the many

volunteers that assisted with sampling. The comments of three anonymous reviewers improved the manuscript.

References

- Abitia-Cardenas, L. A., F. Galvan-Magaña, F. J. Gutierrez-Sanchez, J. Rodriguez-Romero, B. Aguilar-Palomino, and A. Moehl-Hitz. 2000. Diet of blue marlin *Makaira mazara* off the coast of Cabo San Lucas, Baja California Sur, Mexico. *Fisheries Research* 44:95–100.
- Baker, A. N. 1966. Food of marlins from New Zealand waters. *Copeia* 1966:818–822.
- Baum, J. K., and B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Biology* 78:699–714.
- Bizzarro, J. J., H. J. Robinson, C. S. Rinewalt, and D. A. Ebert. 2006. Comparative feeding ecology of four sympatric skate species off central California. *Environmental Biology of Fishes* 80:197–220.
- Botsford, L. W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* 277:509–515.
- Brock, R. E. 1984. A contribution to the trophic biology of the blue marlin (*Makaira nigricans* Lacépède, 1802) in Hawaii. *Pacific Science* 38:141–149.
- Carey, F. G., and R. J. Olson. 1982. Sonic tracking experiments with tunas. ICCAT (International Commission for the Conservation of Atlantic Tunas) Collective Volume of Scientific Papers 17:458–466.
- Carpenter, K. E., editor. 2002. The living marine resources of the western central Atlantic, volumes 1–3. Food and Agriculture Organization of the United Nations, Rome.
- Casazza, T. L., and S. W. Ross. 2008. Fishes associated with pelagic *Sargassum* and open water lacking *Sargassum* in the Gulf Stream off North Carolina. U.S. National Marine Fisheries Service Fishery Bulletin 106:348–368.
- Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54:726–738.
- Cox, S. P., T. E. Essington, J. F. Kitchell, S. J. D. Martell, C. J. Walters, C. Boggs, and I. Kaplan. 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1736–1747.
- De Crespín de Billy, V., S. Doledec, and D. Chessel. 2000. Biplot presentation of diet composition data: an alternative for fish stomach contents analysis. *Journal of Fish Biology* 56:961–973.
- Dragovich, A., and T. Potthoff. 1972. Comparative study of food of skipjack and yellowfin tunas off the coast of West Africa. U.S. National Marine Fisheries Service Fishery Bulletin 70:1087–1109.
- Erdman, D. S. 1962. The sport fishery for blue marlin off Puerto Rico. *Transactions of the American Fisheries Society* 91:225–227.
- Essington, T. E., D. E. Schindler, R. J. Olson, J. F. Kitchell, C. H. Boggs, and R. Hilborn. 2002. Alternative fisheries and the predation rate of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. *Ecological Applications* 12:724–734.
- Evans, J. W. 1961. Normal stages of the early development of the flying fish, *Hirundichthys affinis* (Gunther). *Bulletin of Marine Science of the Gulf and Caribbean* 11:483–502.
- Ferry, L. A., and G. M. Cailliet. 1996. Sample size and data analysis: are we characterizing and comparing diet properly? Pages 71–80 in L. A. Ferry and G. M. Cailliet, editors. *Nutrition in fish: proceedings on the feeding ecology and nutrition in fish*. International Congress on the Biology of Fishes, American Fisheries Society, Physiology Section, Bethesda, Maryland.
- Fine, M. L. 1970. Faunal variation on pelagic *Sargassum*. *Marine Biology* 7:112–122.
- García de los Salmones, R., O. Infante, and J. J. Alio. 1989. Reproducción y alimentación de los peces de pico, *Istiophorus albicans*, *Tetrapturus albidus*, y *Makaira nigricans*, en la costa central de Venezuela. [Reproduction and food of the billfishes, *Istiophorus albicans*, *Tetrapturus albidus*, and *Makaira nigricans* on the coast of central Venezuela.] ICCAT (International Commission for the Conservation of Atlantic Tunas) Collective Volume of Scientific Papers 30:436–439.
- Gotelli, N. J., and G. L. Entsminger. 2001. Ecosim: null models software for ecology, version 6. Burlington, Vermont. Acquired intelligence and kesey-bear. Available: homepages.together.net/~gentsmin/ecosim.htm. (June 2009).
- Graham, B. S., D. Grubbs, K. Holland, and B. N. Popp. 2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Marine Biology* 150:647–658.
- Graves, J. E., B. E. Luckhurst, and E. D. Prince. 2002. An evaluation of pop-up satellite tags for estimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery. U.S. National Marine Fisheries Service Fishery Bulletin 100:134–142.
- Grubbs, R. D., and K. N. Holland. 2003. Yellowfin and bigeye tuna in Hawaii: dietary overlap, prey diversity and the trophic cost of associating with natural and man-made structures. *Proceedings of the 54th Annual International Tuna Conference, Lake Arrowhead, California*. Southwest Fisheries Science Center, National Marine Fisheries Service, and National Oceanic Atmospheric Administration, LaJolla, California.
- Holland, K. N., R. W. Brill, and R. K. C. Chang. 1990. Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. U.S. National Marine Fisheries Service Fishery Bulletin 88:397–402.
- Hyslop, E. J. 1980. Stomach contents analysis: a review of methods and their application. *Journal of Fish Biology* 17:411–429.
- Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? Pages 79–100 in D. J. Stouder, K. L. Fresh, and R. J. Feller, editors. *Theory and application in fish feeding ecology*. University of South Carolina Press, Columbia.
- Juanes, F. 2003. The allometry of cannibalism in piscivorous fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 60:594–602.
- Júnior, T. V., C. M. Vooren, and R. P. Lessa. 2004. Feeding

- habits of four species of *Istiophoridae* (Pisces: Perciformes) from northeastern Brazil. *Environmental Biology of Fishes* 70:293–304.
- Kishinouye, K. 1923. Contributions to the comparative study of the so-called scombroid fishes. *Journal of Tokyo Imperial University College of Agriculture* 8:293–475.
- Krumholz, L. A., and D. P. DeSylva. 1958. Some foods of marlins near Bimini, Bahamas. *Bulletin of the American Museum of Natural History* 114:406–411.
- Kubota, T., and T. Uyeno. 1970. Food habits of lancetfish *Alepisaurus ferox* (Order Myctophiformes) in Suruga Bay, Japan. *Japanese Journal of Ichthyology* 17:22–28.
- Link, J. 2002. What does ecosystem-based fisheries management mean? *Fisheries* 27(4):18–21.
- Maldeniya, R. 1996. Food consumption of yellowfin tuna, *Thunnus albacares*, in Sri Lankan waters. *Environmental Biology of Fishes* 47:101–107.
- Manooch, C. S. III, and W. T. Hogarth. 1983. Stomach contents and giant trematodes from wahoo, *Acanthocybium solandri*, collected along the south Atlantic and gulf coasts of the United States. *Bulletin of Marine Science* 33:227–238.
- Manooch, C. S. III, and D. L. Mason. 1983. Comparative food studies of yellowfin tuna, *Thunnus albacares*, and blackfin tuna, *Thunnus atlanticus* (Pisces: Scombridae) from the southeastern and Gulf coasts of the United States. *Brimleyana* 9:33–52.
- Manooch, C. S. III, D. L. Mason, and R. S. Nelson. 1984. Food and gastrointestinal parasites of dolphin *Coryphaena hippurus* collected along the southeastern and Gulf coasts of the United States. *Bulletin of the Japanese Society of Scientific Fisheries* 50:1511–1525.
- Massutí, E., S. Deudero, P. Sánchez, and B. Morales-Nin. 1998. Diet and feeding of dolphin (*Coryphaena hippurus*) in western Mediterranean waters. *Bulletin of Marine Science* 63:329–341.
- Moteki, M., M. Arai, K. Tsuchiya, and H. Okamoto. 2001. Composition of piscine prey in the diet of large pelagic prey in the eastern tropical Pacific Ocean. *Fisheries Science* 67:1063–1074.
- Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature (London)* 423:280–283.
- NCDMF (North Carolina Division of Marine Fisheries). 2009. North Carolina marine recreational finfish harvest. Available: ncfisheries.net/statistics/recstat/index.html. (June 2009).
- Olson, R. J., and C. H. Boggs. 1986. Apex predation by yellowfin tuna (*Thunnus albacares*): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1760–1775.
- Olson, R. J., and F. Galván-Magaña. 2002. Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean. U.S. National Marine Fisheries Service Fishery Bulletin 100:279–298.
- Oxenford, H. A. 1999. Biology of the dolphinfish (*Coryphaena hippurus*) in the western central Atlantic: a review. *Scientia Marina* 63:277–301.
- Pauly, D., V. Christensen, S. Guénette, T. R. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. *Nature (London)* 418:689–695.
- Rose, C. D., and W. W. Hassler. 1974. Food habits and sex ratios of dolphin *Coryphaena hippurus* captured in the western Atlantic Ocean off Hatteras, North Carolina. *Transactions of the American Fisheries Society* 74:94–100.
- SAFMC (South Atlantic Fishery Management Council). 2003. Fishery management plan for the dolphin and wahoo fishery of the Atlantic. Available: safmc.net/Portals/6/Library/FMP/DolphinWahoo/DolphinWahooFMP.pdf. (June 2009).
- SAFMC (South Atlantic Fishery Management Council). 2009. Interim rule request for red snapper and snapper grouper amendment 17. Available: safmc.net/Portals/6/Library/FMP/SnapGroup/RedSnapperFAQ09.pdf. (June 2009).
- Scharf, F. S., F. Juanes, and R. A. Rountree. 2000. Predator size - prey size relationships of marine fish predators: interspecific variation and the effects of ontogeny and body size on trophic niche breadth. *Marine Ecology Progress Series* 208:229–248.
- Scharf, F. S., F. Juanes, and M. Sutherland. 1998. Inferring ecological relationships from edges of scatter diagrams: comparison of regression techniques. *Ecology* 79:448–460.
- Shimose, T., H. Shono, K. Yokawa, H. Saito, and K. Tachihara. 2006. Food and feeding habits of blue marlin, *Makaira nigricans*, around Yonaguni Island, southwestern Japan. *Bulletin of Marine Science* 79:761–775.
- Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- Schwenke, K. L., and J. A. Buckel. 2008. Age, growth, and reproduction of dolphinfish *Coryphaena hippurus* caught off the coast of North Carolina. U.S. National Marine Fisheries Service Fishery Bulletin 106:82–92.
- Sibert, J., J. Hampton, P. Kleiber, and M. Maunders. 2006. Biomass, size, and trophic status of top predators in the Pacific Ocean. *Science* 314:1773–1776.
- Ter Braak, C. J. F. 1983. Principal components biplots and alpha and beta diversity. *Ecology* 64:454–462.
- Vaske, T. Jr., C. M. Vooren, and R. P. Lessa. 2003. Feeding strategy of yellowfin tuna (*Thunnus albacares*) and wahoo (*Acanthocybium solandri*) in the Saint Peter and Saint Paul Archipelago, Brazil. *Bulletin of the Institute of Fishing* 29:173–181.
- Vecchione, M., C. F. E. Roper, and M. J. Sweeney. 1989. Marine flora and fauna of the eastern United States: Mollusca: Cephalopoda. NOAA Technical Report NMFS 73.
- Wallace, R. K. Jr. 1981. An assessment of diet-overlap indices. *Transactions of the American Fisheries Society* 110:72–76.
- Williams, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C.
- Zavala-Camin, L. A. 1981. Feeding habits and distribution of tuna and their ecological links to other pelagic species of the southeastern and south regions. University of São Paulo, São Paulo, Brazil.

Appendix: Diet Components of North Atlantic Fishes

TABLE A.1.—Stomach contents (by percent frequency of occurrence [%O] and percent weight [%W]) of blue marlins collected from the Big Rock Blue Marlin Tournament in 1998–2000 and 2003–2009. Data on %O were collected from all 10 years of sampling, while data on %W were collected only in 2003–2009. Predator total lengths (TLs) and weights were based on the total number of stomachs analyzed (regardless of whether they contained food or were empty). Values for prey in a row that is headed with a class, order, or family name could not be identified to genus or species.

Taxon	1998	1999	2000	2003		2004	
				%O	%W	%O	%W
Fishes							
Alepisauridae							
Longnose lancet fish <i>Alepisaurus ferox</i>						33.3	6.6
Coryphaenidae							
Dolphinfish <i>Coryphaena hippurus</i>		12.5					
Exocoetidae		12.5	33.3				
Hemiramphidae							
Ballyhoo <i>Hemiramphus brasiliensis</i>	14.3						
Istiophoridae							
Sailfish <i>Istiophorus platypterus</i>							
Lobotidae							
Scombridae	42.8	50.0	55.5	12.5	7.7	33.3	0.5
Bullet mackerel <i>Auxis rochei</i>	28.6	62.5					
Frigate mackerel <i>Auxis thazard</i>	14.3		55.5				
<i>Auxis</i> spp.	14.3	25.0	33.3	87.5	92.3	66.7	92.9
King mackerel <i>Scomberomorus cavalla</i>			11.1				
Atlantic mackerel <i>Scomber scombrus</i>	14.3						
Unknown fish	14.3	12.5					
Invertebrates							
Cephalopoda	14.3	12.5					
Argonautidae							
Octopodida		12.5					
Teuthida							
Predator information							
Total stomachs analyzed	10	8	9	8		3	
Stomachs containing prey	7	8	9	8		3	
Mean (SE) predator TL (cm)	356 (6)	367 (3)	360 (10)	364 (5)		360 (9)	
Predator TL range (cm)	335–387	354–378	338–421	333–377		351–378	
Mean (SE) predator weight (kg)	194 (12.3)	225 (7.4)	209 (25.0)	241 (14.5)		217 (18.5)	

TABLE A.1.—Extended.

Taxon	2005		2006		2007		2008		2009	
	%O	%W	%O	%W	%O	%W	%O	%W	%O	%W
Fishes										
Alepisauridae										
Longnose lancet fish	14.3	0.1								
Coryphaenidae										
Dolphinfish	14.3	3.4			28.6	51.3			20.0	24.1
Exocoetidae										
Hemiramphidae										
Ballyhoo										
Istiophoridae										
Sailfish									20.0	1.7
Lobotidae							16.7	28.7		
Scombridae			33.3	24.3			16.7	11.0	40.0	70.2
Bullet mackerel										
Frigate mackerel										
<i>Auxis</i> spp.	85.7	92.2	66.7	73.1	85.7	48.7	66.7	60.0		
King mackerel										
Atlantic mackerel										
Unknown fish	14.3	4.2	33.3	0.9						
Invertebrates										
Cephalopoda										
Argonautidae	14.3	0.1								
Octopodida										
Teuthida			33.3	1.6			16.7	0.2	40.0	4.0
Predator information										
Total stomachs analyzed	8		6		7		6		5	
Stomachs containing prey	7		6		7		6		5	
Mean (SE) predator TL (cm)	363 (2)		349 (6)		368 (6)		376 (5)		332 (14)	
Predator TL range (cm)	355–371		330–368		351–394		361–396		282–363	
Mean (SE) predator weight (kg)	223 (5.6)		199 (9.4)		214 (17.0)		243 (12.7)		187.7 (12.5)	

TABLE A.2.—Stomach contents (by percent frequency of occurrence [%O] and percent weight [%W] of dolphinfish collected from the Big Rock Blue Marlin Tournament in 1998–2000 and 2003–2009. Data on %O were collected from all 10 years of sampling, while data on %W were collected only in 2003–2009. Predator total lengths (TLs) and weights were based on the total number of stomachs analyzed (regardless of whether they contained food or were empty). Values for prey in a row that is headed with a class, order, or family name could not be identified to genus or species.

Taxon	1998	1999	2000	2003		2004	
				%O	%W	%O	%W
Fishes							
Balistidae				6.9	10.3	12.0	4.2
Gray triggerfish <i>Balistes capriscus</i>				6.9	2.7		
<i>Balistes</i> spp.				3.4	12.9		
Ocean triggerfish <i>Canthidermis sufflamen</i>							
Belontiidae						4.0	2.6
Flat needlefish <i>Ablennes hians</i>				3.4	0.2		
Caristiidae							
Manefish <i>Caristius maderensis</i>							
Carangidae				10.3	1.5	4.0	0.4
Blue runner <i>Caranx crysos</i>							
<i>Caranx</i> spp.							
Rough scad <i>Trachurus lathamii</i>				3.4	0.2		
Cottonmouth jack <i>Uraspis secunda</i>							
Coryphaenidae							
Dolphinfish	25.0	40.0	41.7	3.4	1.3	4.0	24.9
Dactylopteridae							
Flying gurnard <i>Dactylopterus volitans</i>							
Diodontidae							
Balloonfish <i>Diodon holocanthus</i>	16.7	20.0	8.3			20.0	3.8
Porcupinefish <i>Diodon hystrix</i>						4.0	1.3
<i>Diodon</i> spp.	16.7	20.0					
Exocoetidae			8.3	6.9	3.9	8.0	3.7
Margined flyingfish <i>Cheilopogon cyanopterus</i>				3.4	8.9		
Clearwing flyingfish <i>Cypselurus comatus</i>							
Oceanic two-wing flyingfish <i>Exocoetus obtusirostris</i>							
<i>Exocoetus</i> spp.							
Fourwing flyingfish <i>Hirundichthys affinis</i>	16.7						
Sailfin flyingfish <i>Parexocoetus brachypterus</i>							
Flyingfish <i>Parexocoetus hillianus</i>							
Istiophoridae							
Sailfish							
Kyphosidae							
Bermuda chub <i>Kyphosus sectatrix</i>							
Monacanthidae	8.3						
Orange filefish <i>Aluterus schoepfii</i>							
Fringed filefish <i>Monacanthus ciliatus</i>							
Planehead filefish <i>Stephanolepis hispidus</i>			16.7			4.0	0.2
Pygmy filefish <i>Stephanolepis setifer</i>	8.3						
Scombridae				3.4	2.5	12.0	34.6
<i>Auxis</i> spp.				6.9	25.3	4.0	2.8
Scorpaenidae							
<i>Scorpaena</i> spp.							
Stromateidae							
Gulf butterflyfish <i>Peprius burti</i>				3.4	0.8		
Syngnathidae							
Longsnout seahorse <i>Hippocampus reidi</i>				6.9	0.1		
<i>Hippocampus</i> spp.				13.8	0.2	4.0	<0.1
Sargassum pipefish <i>Syngnathus pelagicus</i>							
<i>Syngnathus</i> spp.						4.0	0.1
Tetraodontidae						4.0	
Smooth puffer <i>Lagocephalus laevigatus</i>	8.3		8.3				
Oceanic puffer <i>Lagocephalus lagocephalus</i>	8.3			3.4	10.9		
<i>Lagocephalus</i> spp.	8.3						
Unknown fish	33.3	60.0	50.0	37.9	5.5	48.0	7.8
Invertebrates							
Cephalopoda	16.7						
Argonautidae							
Octopodida	8.3		8.3				
Teuthida		20.0		3.4	<0.1	4.0	6.3

TABLE A.2.—Extended.

Taxon	2005		2006		2007		2008		2009	
	%O	%W								
Fishes										
Balistidae	22.2	6.7	4.3	1.8			12.2	0.7		
Gray triggerfish			2.2	2.7						
<i>Balistes</i> spp.										
Ocean triggerfish							4.1	6.5		
Belonidae										
Flat needlefish										
Caristiidae										
Manefish									2.4	1.4
Carangidae	5.6	2.1	8.7	1.0					2.4	0.9
Blue runner									2.4	0.7
<i>Caranx</i> spp.									2.4	0.1
Rough scad										
Cottonmouth jack							4.1	0.1		
Coryphaenidae										
Dolphinfish	2.8	11.3	10.9	50.3			10.2	44.6	4.8	2.0
Dactylopteridae										
Flying gurnard							2.0	<0.1	4.8	0.1
Diodontidae	2.8	0.2	4.3	0.3					4.8	0.4
Balloonfish	38.9	11.1	4.3	0.2						
Porcupinefish							2.0	<0.1		
<i>Diodon</i> spp.	33.3	6.7	2.2	<0.1						
Exocoetidae	5.6	4.2	13.0	6.7	14.3	19.3	16.3	9.0	16.7	22.6
Margined flyingfish	2.8	3.7								
Clearwing flyingfish			2.2	1.6						
Oceanic two-wing flyingfish							2.0	0.3		
<i>Exocoetus</i> spp.			2.2	1.1						
Fourwing flyingfish	2.8	3.6								
Sailfin flyingfish			4.3	2.9						
Flyingfish			4.3	3.4			2.0	2.2		
Istiophoridae							2.0	0.1	2.4	<0.1
Sailfish									2.4	0.3
Kyphosidae										
Bermuda chub	2.8	3.1								
Monacanthidae					7.1	<0.1			9.5	4.2
Orange filefish			2.2	0.5						
Fringed filefish									4.8	12.6
Planehead filefish			6.5	0.9						
Pygmy filefish									9.5	0.3
Scombridae							10.2	19.0	2.4	0.4
<i>Auxis</i> spp.			4.3	1.7					2.4	1.6
Scorpaenidae										
<i>Scorpaena</i> spp.	2.8	1.5								
Stromateidae									2.4	<0.1
Gulf butterflyfish										
Syngnathidae										
Longsnout seahorse										
<i>Hippocampus</i> spp.					7.1	0.2			11.9	5.5
Sargassum pipefish									2.4	<0.1
<i>Syngnathus</i> spp.										
Tetraodontidae							2.0	0.5	2.4	0.1
Smooth puffer										
Oceanic puffer	2.8	30.0	2.2	0.3						
<i>Lagocephalus</i> spp.							2.0	4.3		
Unknown fish	38.9	7.3	54.3	16.2	35.7	4.9	40.8	5.1	47.6	10.0
Invertebrates										
Cephalopoda	2.8	2.7	6.5	<0.1					11.9	1.1
Argonautidae			17.4	0.8	7.1	<0.1	4.1	0.2	21.4	3.3
Octopodida										
Teuthida	5.6	<0.1	21.7	2.9	14.3	58.6	20.4	1.9	4.8	0.1

TABLE A.2.—Extended and continued.

Taxon	2005		2006		2007		2008		2009	
	%O	%W	%O	%W	%O	%W	%O	%W	%O	%W
Crustacea	8.3	5.7	4.3	<0.1						
Decapoda							6.1	0.1		
Gerridae			2.2	<0.1						
Isopoda			2.2	<0.1			2.0	0.1		
Naticidae							2.0	<0.1		
Portunidae	36.1	4.1	26.1	0.9	14.3	1.3	55.1	4.8	71.4	17.3
Scyllaridae									2.4	0.1
Sicyoniidae	2.8	0.7	2.2	0.2	7.1	2.1	2.0	0.2		
	Vegetation									
Shoal grass					7.1	<0.1				
Red mangrove			2.2	<0.1	7.1	0.5				
Algae	27.8	0.8	15.2	0.8	35.7	5.3	18.4	0.3	50.0	13.9
Manatee grass					7.1	<0.1	2.0	<0.1	4.8	<0.1
Turtle grass							2.0	<0.1		
Other vegetation					14.3	7.3	2.0	<0.1	16.7	0.9
	Other diet items									
Plastic					14.3		4.1			
Styrofoam					7.1					
Unidentified			2.2		7.1				16.7	
	Predator information									
Total stomachs analyzed	40		54		15		54		43	
Stomachs containing prey	36		46		14		49		42	
Mean (SE) predator TL (cm)	138 (2)		138 (2)		126 (3)		134 (2)		130 (3)	
Predator TL range (cm)	123–169		114–163		109–151		104–164		95–168	
Mean (SE) predator weight (kg)	13.9 (0.7)		14.0 (0.7)		10.7 (0.7)		13.9 (0.8)		23.0 (3.4)	

TABLE A.3.—Stomach contents (by percent frequency of occurrence [%O] and percent weight [%W]) of yellowfin tuna collected from the Big Rock Blue Marlin Tournament in 1998–2000 and 2003–2009. The %O data were collected from all 10 years of sampling, while %W data were collected only in 2003–2009. Predator total lengths (TLs) and weights were based on the total number of stomachs analyzed (regardless of whether they contained food or were empty). Values for prey in a row that is headed with a class, order, or family name could not be identified to genus or species.

Taxon	1998	1999	2000	2003		2004	
				%O	%W	%O	%W
Fishes							
Clupeidae							
Atlantic menhaden <i>Brevoortia tyrannus</i>							
Dactylopteridae							
Flying gurnard							
Diodontidae							
Balloonfish	28.6						
<i>Diodon</i> spp.		11.1					
Exocoetidae		11.1	60.0	20.0	7.7	33.3	87.3
Clearwing flyingfish			20.0				
<i>Cypselurus</i> spp.							
<i>Exocoetus</i> spp.							
Fourwing flyingfish		11.1					
<i>Parexocoetus hillianus</i>							
Hemiramphidae							
Ballyhoo			20.0				
Monacanthidae	28.6						
Planehead filefish			20.0				
Scombridae	28.6		20.0	20.0	12.5		
Bullet mackerel							
Frigate mackerel							
<i>Auxis</i> spp.			20.0	60.0	76.0		
Atlantic mackerel			20.0				
Syngnathidae							
<i>Hippocampus</i> spp.				20.0	<0.1		
Tetraodontidae							
Unknown fish	57.1	33.3	40.0	20.0	2.5	66.7	5.0
Invertebrates							
Cephalopoda	14.3						
Argonautidae	14.3		20.0				
Octopodida	71.4	22.2	60.0				
Teuthida	100	66.7	40.0	20.0	1.3	33.3	2.1
Crustacea		11.1	20.0				
Decapoda						66.7	0.2
Portunidae							
Sicyoniidae							
Vegetation							
<i>Sargassum</i> spp.						100	5.4
Turtle grass							
Other vegetation							
Other diet items							
Plastic							
Unidentified							
Predator information							
Total stomachs analyzed	7	10	5	5		3	
Stomachs containing prey	7	9	5	5		3	
Mean (SE) predator TL (cm)	122 (7)	118 (3)	121 (7)	110 (6)		117 (4)	
Predator TL range (cm)	113–130	107–137	107–143	91–121		110–121	
Mean (SE) predator weight (kg)	25.8 (5.2)	22.3 (1.4)	25.5 (4.3)	18.6 (3.0)		21.4 (2.2)	

TABLE A.3.—Extended.

Taxon	2005		2006		2007		2008		2009	
	%O	%W	%O	%W	%O	%W	%O	%W	%O	%W
Fishes										
Clupeidae										
Atlantic menhaden <i>Brevoortia tyrannus</i>			28.6	21.2						
Dactylopteridae										
Flying gurnard									11.1	<0.1
Diodontidae										
Balloonfish										
<i>Diodon</i> spp.										
Exocoetidae	50.0	51.2	14.3	15.6					55.6	13.3
Clearwing flyingfish										
<i>Cypselurus</i> spp.	37.5	36.2								
<i>Exocoetus</i> spp.									11.1	1.0
Fourwing flyingfish										
<i>Parexocoetus hillianus</i>			14.3	9.8						
Hemiramphidae										
Ballyhoo										
Monacanthidae										
Planehead filefish										
Scombridae							100	35.8	33.3	18.6
Bullet mackerel									11.1	15.2
Frigate mackerel									11.1	13.3
<i>Axix</i> spp.			14.3	32.8						
Atlantic mackerel										
Syngnathidae										
<i>Hippocampus</i> spp.										
Tetraodontidae									11.1	0.3
Unknown fish	50.0	8.8	42.9	16.1	50.0	91.8	100	38.4	55.6	4.4
Invertebrates										
Cephalopoda									22.2	0.2
Argonautidae					25.0	8.2				
Octopodida										
Teuthida			42.9	4.4			100	24.8	44.4	35.5
Crustacea										
Decapoda										
Portunidae	12.5	<0.1							11.1	<0.1
Sicyoniidae									11.1	0.1
Vegetation										
<i>Sargassum</i> spp.	12.5	3.7							11.1	<0.1
Turtle grass									11.1	<0.1
Other vegetation									33.3	0.1
Other diet items										
Plastic			14.3							
Unidentified									11.1	
Predator information										
Total stomachs analyzed	11		7		4		1		9	
Stomachs containing prey	7		6		3		1		9	
Mean (SE) predator TL (cm)	106 (6)		118 (5)		123 (7)		111 (0)		112 (5)	
Predator TL range (cm)	93–163		100–130		103–136		–		83–141	
Mean (SE) predator weight (kg)	16.0 (3.5)		21.6 (2.5)		25.2 (3.5)		15.5 (0)		23.0 (3.4)	

TABLE A.5.—Continued.

Taxon	Jan (1)		Mar (1)		Apr (2)		May (3)		Jun (2)	
	%O	%W	%O	%W	%O	%W	%O	%W	%O	%W
Coryphaenidae										
Dolphinfish									5.2	<0.1
Dactylopteridae										
Flying gurnard					7.1	0.1				
Exocoetidae			66.7	77.0	35.7	50.9	18.6	21.4	23.1	29.0
Sailfin flyingfish										
Diodontidae							6.8	1.4	7.7	0.2
Balloonfish					7.1	0.5	22.0	18.3	2.6	0.6
Istiophoridae										
Lobotidae										
Atlantic tripletail <i>Lobotes surinamensis</i>										
Monacanthidae					14.3	1.1	11.9	1.6	12.8	1.4
Orange filefish									2.6	11.4
Scrawled filefish <i>Aluterus scriptus</i>										
Planehead filefish							5.1	0.4	5.2	3.5
Mugilidae										
White mullet <i>Mugil curema</i>									2.6	<0.1
Mullidae							1.7	<0.1		
Dwarf goatfish <i>Upeneus parvus</i>									2.6	<0.1
Scombridae							3.4	7.7		
<i>Auxis</i> spp.							1.7	8.3	2.6	16.8
Syngnathidae										
<i>Hippocampus</i> spp.	100	2.7			35.7	8.7	18.6	4.5	10.2	0.3
Northern pipefish <i>Syngnathus fuscus</i>										
Tetraodontidae							3.4	0.5	2.6	0.1
Oceanic puffer										
<i>Sphoeroides</i> spp.										
Uranoscopidae										
Southern stargazer <i>Astroscopus y-graecum</i>					7.1	0.9				
Xiphiidae										
Swordfish <i>Xiphias gladius</i>							1.7	0.3		
Unidentified fish	100	48.0	33.3	23.0	57.1	13.0	54.3	13.5	66.7	6.7
Invertebrates										
Cephalopoda							1.7	0.2	2.6	2.5
Argonautidae					21.4	1.2	1.7	0.2		
Teuthida					21.4	5.7	8.5	0.2	7.7	1.1
Crustacea										
Decapoda							1.7	<0.1	12.8	1.4
Portunidae	100	24.5					13.6	1.4	15.4	2.0
Sicyoniidae							1.7	0.2	7.7	2.3
Vegetation										
<i>Sargassum</i> spp.					57.1	12.6	33.8	6.4	7.7	3.0
Other diet items										
Plastic							1.7			
Predator information										
Total stomachs analyzed	1		17		41		83		58	
Stomachs containing prey	1		3		14		59		39	
Mean (SE) predator TL (cm)	88 (0)				92 (3)		106 (3)		103 (4)	
Predator TL range (cm)					52–129		57–158		56–159	
Mean (SE) predator weight (kg)	3.2 (0)				4.6 (0.4)		7.8 (0.7)		8.7 (1.0)	

TABLE A.5.—Extended and continued.

Taxon	Jul (2)		Aug (2)		Sep (2)		Oct (2)		Nov (1)	
	%O	%W	%O	%W	%O	%W	%O	%W	%O	%W
Coryphaenidae										
Dolphinfish			2.9	19.5						
Dactylopteridae										
Flying gurnard	2.2	0.1								
Exocoetidae	13.3	6.5			13.0	18.2				
Sailfin flyingfish					4.3	1.8				
Diodontidae	2.2	0.1	2.9	1.0						
Balloonfish	2.2	10.3					8.3	1.3		
Istiophoridae	2.2	<0.1								
Lobotidae										
Atlantic tripletail			2.9	2.9						
Monacanthidae	2.2	0.7	14.7	7.3	8.7	6.6	8.3	0.8		
Orange filefish					2.9	5.5				
Scrawled filefish	20.0	2.4			8.7	5.9				
Planehead filefish	11.1	3.3	11.8	4.3	4.3	0.2				
Mugilidae										
White mullet										
Mullidae										
Dwarf goatfish										
Scombridae	2.2	<0.1								
<i>Auxis</i> spp.	2.2	3.2			4.3	12.3				
Syngnathidae										
<i>Hippocampus</i> spp.			11.8	0.2	4.3	0.2				
Northern pipefish			5.9	0.1						
Tetraodontidae	8.9	3.8	8.8	11.3						
Oceanic puffer	2.2	18.0								
<i>Sphoeroides</i> spp.			2.9	<0.1						
Uranoscopidae										
Southern stargazer										
Xiphiidae										
Swordfish										
Unidentified fish	60.0	24.8	70.6	19.4	56.5	35.0	58.3	56.5	100	38.5
			Invertebrates							
Cephalopoda	2.2	6.6			4.3	2.0			100	61.5
Argonautidae										
Teuthida	6.7	1.6	17.6	5.4	4.3	0.5	16.7	9.6		
Crustacea										
Decapoda	8.9	0.2	8.8	0.1						
Portunidae	13.3	1.7	2.9	0.1	4.3	0.1				
Sicyonidae										
			Vegetation							
<i>Sargassum</i> spp.	44.4	1.6	41.2	1.3	21.7	2.9	33.3	2.4		
			Other diet items							
Plastic										
			Predator information							
Total stomachs analyzed	56		73		48		39		4	
Stomachs containing prey	45		34		23		12		1	
Mean (SE) predator TL (cm)	76 (4)		75 (3)		67 (3)		70 (3)		66 (4)	
Predator TL range (cm)	24–145		35–146		35–105		51–170		57–75	
Mean (SE) predator weight (kg)	2.8 (0.6)		2.2 (0.5)		2.0 (0.2)		3.5 (1.2)		1.6 (0.3)	